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I acknowledge your help: capuchin monkeys' sensitivity to others' labor

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Our society is sustained by wide-ranging cooperation. If individuals are sensitive to others' gains and losses as well as the amount of labor, they can ensure future beneficial cooperative interaction. However, it is still an open question whether nonhuman primates are sensitive to others' labor. We asked this question in tufted capuchin monkeys in an experimental food-sharing situation by comparing conditions with labor by two participants equalized (Equal labor condition) or unequalized (Unequal labor condition). The operator monkey pulled the drawer of one of two food containers placed between two monkeys, each containing a food for him/herself and another for the recipient monkey. The recipient received either high- or low-value food depending on the operator's choice, whereas the operator obtained the same food regardless of his/her choice. In Unequal labor condition, the operator first had to pull the handle of the board to which the containers were glued, and then pull the drawer of one of the containers, while the recipient received food with no labor. In Equal labor condition, the recipient had to pull the handle of the board so that the operator could operate a container. Results showed that operators chose the high-value food container for recipients more often than when the recipient was absent only in Equal labor condition. This suggests that capuchin monkeys are sensitive to others' labor and actively give food to a partner who has helped them to complete a task. (237 words)

Introduction

Human social organization depends on cooperation with others (Boyd and Richerson 2005). Cooperation yields greater benefits than those that can be achieved by individual effort alone. Human cooperation appears to be maintained in part by prosocial orientations and a concern about inequity.

Cooperation is in fact widespread in nonhumans (see Dugatkin 1997). In particular, several species of nonhuman primates have been demonstrated to show elaborate cooperative behaviors in the laboratory [e.g., chimpanzees (*Pan troglodytes*): Crawford 1937; Hirata and Fuwa 2007; Melis et al. 2006ab, capuchin monkeys (*Cebus apella*): Brosnan et al. 2006; de Waal and Berger 2000; Hattori et al. 2005, cotton-top tamarins (*Saguinus oedipus*): Cronin et al. 2005, 2008]. This may suggest that human-like cooperation has traceable evolutionary roots.

Individuals are able to ensure future beneficial cooperative interaction, on the ground that they are not only sensitive to gains and losses but also able to compare their own effort and reward with others', that is, they have inequity aversion (IA). IA probably evolved over a series of simpler, intermediate steps in nonhuman primates. In Brosnan and de Waal (2003), brown capuchin monkeys apparently eschewed imbalance of reward and effort between participants in token exchanges with a human experimenter. The monkeys willingly exchanged tokens for a piece of cucumber at first, but they started to refuse the exchange or to accept the food after witnessing their partner receiving better food (a grape) for the same token. Such refusals increased when the partner received a grape without exchanging the token. Brosnan et al. (2005) and Brosnan et al. (2010b) replicated these results in chimpanzees (but see Bräuer et al. 2009), although they did not appear to respond to the discrepancy between their own

effort and others'.

In this regard, however, several researchers have suggested that simpler cognitive mechanisms might explain the results of these studies (see Bräuer et al. 2006; Dubreuil et al. 2006; Henrich 2004; Silberberg et al. 2009; Roma et al. 2006; Wynne 2004). For example, Roma et al. (2006) argued that the apparent aversion to inequity shown by Brosnan & de Waal (2003) might be explained by frustration due to an individual's past experience with greater rewards (but see Brosnan & de Waal 2006). On the other hand, Dindo and de Waal (2007) reported that no IA effect occurred when they gave free rewards to the monkeys as Bräuer et al. (2006), Dubreuil et al. (2006) and Roma et al. (2006) tasks, in which both the subject and the partner just determined whether they would accept a reward offered by the human experimenter without any labor. That is, they suggest that some labor is necessary to show IA. In addition, van Wolkenten et al. (2007) countered many of the alternative hypotheses, such as the greed and frustration accounts, by using a task requiring labor in both the subject and the partner in which IA was confirmed. Recently, however, Bräuer et al. (2009) failed to reproduce the findings of Brosnan et al. (2005) in great apes using the same procedure. Thus, the extent of IA in cooperative nonhuman primates remains open to debate.

Therefore, first, it must be investigated whether cooperative nonhuman primates have essential components to have IA, that is, sensitivity to others' reward and their labor. Most of recent relevant studies with various primates have focused only on sensitivity to others' rewards, that is, other-regarding preferences, which underlie prosociality in humans (see de Waal and Suchak 2010). Several studies explicitly designed to look for prosocial preferences in chimpanzees found no evidence that they behave in ways that benefit their partners, even when it costs them nothing; that is, they

were indifferent to others' rewards (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008, Yamamoto & Tanaka 2010). On the other hand, capuchin monkeys have showed sensitivity to others' rewards and other-regarding preferences in experimental food-sharing tasks (Lakshminarayanan & Santos 2008, Takimoto et al. 2010), a token exchange task (de Waal et al. 2008) and a bar-pull task (Brosnan et al. 2010a). Among other New World monkeys, common marmosets spontaneously provide food to nonreciprocating and genetically unrelated individuals (Burkart et al. 2007). Moreover, cottontop tamarins show sensitivity to others' rewards and a stronger reaction to inequity when they complete a task than when they do not (Neiworth et al. 2009; but see Cronin et al. 2008, 2009; Stevens 2010). It has been proposed that other-regarding preferences might be found in species that rely on cooperative strategies, such as cooperative breeding (Clutton-Brock 2002). Most recently, however, Brosnan et al. (2010b) showed that chimpanzees were more likely to refuse a high-value grape when another chimpanzee got a lower-value carrot than when the other chimpanzee also received a grape. In other words, chimpanzees avoided inequity which was advantageous for them, and showed other-regarding preference. Additionally, Melis et al. (in press) reported that chimpanzees helped their conspecifics obtain even food items, that is, the presence of food did not constrain chimpanzees' tendency to help others. Moreover, Hare & Kwetuenda (2010) reported that bonobos (*Pongo pygmaeus*) preferred to release a partner from an adjacent room and eat together instead of eating all the food alone. Together these studies suggest that sensitivity to others' rewards, in particular other-regarding preferences, is not unique to cooperative breeders but may be seen broadly among cooperating nonhuman primates.

By comparison, there are very few studies on nonhuman primates' sensitivity

to others' labor. In de Waal & Berger (2000), pairs of capuchin monkeys were required to combine efforts to pull a tray with food. The capuchins more successfully cooperated when presented with a tray baited for both monkeys than when presented with a tray baited for only one. Moreover, significantly more pieces of food were shared after successful cooperation trials than after solo-effort trials. A greater portion of food transfers after cooperation were of a tolerant nature. However, an increase in proximity between the monkeys could have led to more food sharing as a byproduct, rather than as the intention of the operator. Moreover, it remains unclear whether experience of partners' cooperative labor leading to food would influence possessors' subsequent food sharing. Capuchin monkeys also showed sensitivity to their own effort and responded to inequity by modifying their effort to obtain food (van Walkenten et al. 2007). That is, capuchins increasingly refused a token or food when the effort required to obtain a reward increased. However, it was not clear if the subject monkeys were sensitive to their partners' effort because the partner monkey always received food without any effort. Thus, it is still an open question whether nonhuman primates are capable of recognizing others' effort and of comparing the cost/benefit relationship between self and others.

In the present study, we investigated whether capuchin monkeys are sensitive to others' labor and its disparity between the participants (the operator and the recipient). We changed the amount of each participant's labor required to obtain food in an experimentally induced cooperative food-sharing situation. We expected situations that required labor in both participants to facilitate their sensitivity to others' reward and labor. The operators were able to give either high- or low-value food to recipients. The operators received the same high-value food regardless of their choices. Therefore, the

operators' choice of the high-value container for the recipient should indicate intentional giving of the high-value food and allow us to rule out giving as a by-product of the operator obtaining his/her own food. We also investigated whether experience of recipients' cooperative labor leading to food would influence operators' subsequent food choices by setting two Unequal labor conditions and conducting each Unequal labor condition before and after Equal labor condition.

We manipulated the following 3 experimental parameters: the presence of the recipient (Faced or Alone condition), the recipient's social rank (Dominant or Subordinate recipient condition), the subjects' labor (Unequal labor 1, Equal labor or Unequal labor 2 condition). In Unequal labor 1 and 2 conditions, the operator first had to pull the handle of the board on which the two food containers were glued and then pull the drawer of one of the containers, while the recipient obtained food without any labor. In contrast, Equal labor condition was a cooperative food sharing situation in which the recipient first had to pull the handle of the board in order to reposition the containers so that the operator could select one by pulling the drawer. If operators are sensitive to others' labor and can compare it with their own, they should preferentially choose the high-value container in Equal labor condition, but not in Unequal labor 1 and 2 conditions, of Faced, not Alone, conditions. In addition, once operators had experience of recipients having to work in order to receive rewards, the operators may become frustrated if the recipients obtain rewards without any labor (Unequal labor 2 condition). If the sight of the previously helpful partner now free-riding is negative for the operator, he/she should choose the high-value container more frequently in Unequal labor 1 condition than Unequal labor 2 condition.

Tufted capuchin monkeys are phyletically more distant from humans than

chimpanzees are, but they are suitable for such work in view of suggested IA (Brosnan and de Waal 2003; Brosnan et al. 2010a; Fletcher 2008; van Wolkenten et al. 2007) and robust prosociality (Brosnan et al. 2010a; de Waal et al. 2008; Lakchminarayanan and Santos 2008; Takimoto et al. 2010) of this species. Furthermore, capuchins are tolerant to the extent that they actively share high-value food especially with subordinates (Takimoto et al. 2010). This social background creates a baseline level of expectation of equity that makes individuals more likely to react to inequitable situations (Brosnan 2006; de Waal 1996). Anderson (2007) suggested that more tolerant primates are more likely to show cooperation, and capuchin monkeys show some elaborate cooperative behaviors, linked to reciprocity and food sharing, both in the wild and in captivity (see de Waal and Suchak 2010).

Method

Participants

Participants were six tufted capuchin monkeys (*Cebus apella*), housed together in a group of seven at the Graduate School of Letters, Kyoto University. Heiji (male) and Zilla (female) were 15 years old, Kiki (female) and Theta (female) were 13 years old, Pigmon (male) was 11 years old and Zinnia (male) was 8 years old. All subjects except Zinnia, who was born to Heiji and Zilla in the laboratory, were born and raised in a social group at the Primate Research Institute, Kyoto University. The dominance hierarchy among these monkeys was very stable, confirmed through daily observations and occasional pairwise dominance tests using food competition. Heiji was the alpha male, while Theta was the most subordinate in the group. These two individuals served as recipients. In decreasing order of dominance, the others, who served as operators,

were ranked as follows: Pigmon, Zinnia, Zilla, and Kiki.

All monkeys had experienced a variety of laboratory tests on topics such as operant discrimination (Fujita 2004; Fujita and Giersch 2005), tool use (Fujita et al. 2003; Fujita et al. in press), deception (Fujita et al. 2002), cooperation (Hattori et al. 2005), social knowledge (Anderson et al. 2004; Anderson et al. 2005a,b; Anderson et al. 2008; Anderson et al. 2010; Hattori et al. 2007; Hattori et al. 2010; Kuroshima et al. 2002; Kuroshima et al. 2003; Kuroshima et al. 2008; Morimoto and Fujita in press), mirror-image stimulation (Paukner et al. 2004), and video-image stimulation (Anderson et al. 2009). The monkeys were not food deprived but received a portion of their daily rations during testing and the remainder in their home cage after testing each day. Kiki was pregnant and gave birth during the experiment, but she failed to care for the baby and so her baby was hand-raised; Kiki therefore continued to participate in the study.

Apparatus

Figures 1a and 1b

Two experimental cages, 60 cm (W) x 45 cm (D) x 55 cm (H), made of transparent acrylic with a wire-mesh floor were placed facing each other across a wooden table, 80 cm (W) x 39 cm (D) x 74 cm (H) (Figure 1). An operator monkey was placed in one cage which had three round openings (3.5 cm in diameter) aligned horizontally in the front panel. These openings were 6 cm apart from each other and 10.5 cm from the floor. A recipient monkey was placed in the other cage which had a front panel opening of 24 cm (W) x 3 cm (H). This opening was positioned centrally

and 8.5 cm from the floor. Each cage was set on a metallic pedestal of 65 cm (W) x 56 cm (D) x 74cm (H).

Two identical food containers, 9.5 cm (W) x 16 cm (D) x 10.5 cm (H), made of transparent acrylic were placed 12cm apart on a transparent acrylic board, 58cm(W)x 30cm(D), on the wooden table between the two cages (Figure 1). The containers could slide along two metallic rails 58cm apart on a white plastic board, 58cm (W) x 41cm (D). The containers had a drawer, 9 cm (W) x 8 cm (D) x 3.5 cm (H) at the operator side, 6 cm from the bottom. When pulled, the drawer, containing a food item, slid out to within reach of the operator monkey and this also dispensed food to the recipient by hitting a dropper board attached behind the drawer. The operator was allowed to pull only one drawer at a time. The recipient had no means of operating the drawer, and hence was a passive recipient of food.

The precise placement of the containers and the handle of the board on which the containers were fixed varied as a function of the labor conditions. For Unequal labor 1 and 2 conditions the containers were set out as shown in Figure 1a. The containers were placed out of reach of the operator, but the handle (W20cm×D0.5cm×H4cm) was either 10 cm or 14cm from the operator, determined by the operator's arm length. Thus the operator could pull the containers to within reach. For Equal labor condition the containers were set out as shown in Figure 1b. Now, the handle was within reach of the recipient (either 12 cm or 14 cm depending on the recipient). Additionally, the containers were moved 22 cm nearer to the operator's box, so that the operator could not pull on a drawer due to inadequate space.

A transparent screen, 50 cm (W) x 28 cm (H), was placed against each cage to prevent the monkeys from handling the containers during inter-trial intervals and the

241 baiting process.

242 All tests were recorded on two digital video cameras (Sony, DCR-TRV27), one
243 located behind the recipient to record the operator's behavior and the other located
244 behind the operator to record the recipient's behavior.

245

246 Procedure

247

248 **Food preference test**

249 We conducted a food preference test to determine appropriate food rewards for
250 all participants. Their preference between a piece of peanut and a few leaves of parsley
251 was tested by a two-choice task. All of them showed a clear preference for the peanut
252 over the parsley (12 choices out of the 12 trials). We thus decided to use peanut as a
253 high-value food reward and parsley as a low-value reward in this experiment.

254

255 **Preliminary training**

256 The 4 operator monkeys had been trained to operate the food containers in the
257 previous study (Takimoto et al. 2010). Therefore, they had learned that they were able
258 to obtain food in the drawer of the container by pulling it within 30 seconds. They also
259 had learned that the recipient monkey was able to collect food without any labor by the
260 operator's pulling. Moreover, they had learned that they were able to obtain only their
261 own food, not the food dropped on the recipient's side irrespective of the
262 presence/absence of the recipient (see Takimoto et al. 2010 for details).

263 In the preliminary training for operators before testing, all 4 operators were
264 individually trained to obtain food by completing the sequence of pulling the handle of

the board and operating one of the two food containers. They were trained until they performed these operations within 30 sec at 80% level in five consecutive sessions (1 session = 12 trials). Each operator participated in this training a session per day. This training required between 5 and 11 days.

In the preliminary training for recipients before testing in Equal labor condition, both recipients were individually trained to obtain a chance to receive food by pulling the handle of the board to enable the operator's pulling the drawers, in the absence of the operator. The experimenter pulled the drawer of the food container in place of the operator, which prevented the recipient's experience of the interaction with the particular operator in the training from influencing the test results. The recipients were trained until they started the operation within 30 sec at 80% level in five consecutive sessions (1 session = 12 trials). Each recipient participated in this training a session per day. This training required 7 sessions.

Test

Figure 2

The experimenter placed a transparent screen against the front panel of each cage. She then baited the two food containers. Following this, as soon as the operator looked toward the containers, the experimenter removed both screens simultaneously and the trial started. The operator chose one of two food containers and pulled the drawer of the container. The operator received the same high-value food whichever container he/she chose, whereas the recipient received either high- or low-value food

289 depending upon the operator's choice. The trial ended when the recipient picked up the
290 food or in 10 sec after the operator's choice. During the inter-trial interval of 30 s, the
291 experimenter removed any leftover food and set the containers up for the next trial.
292 As described earlier, we varied three experimental parameters: (i) presence of
293 the recipient, (ii) social rank of the recipient and (iii) labor of the two individuals (the
294 operator and the recipient). Regarding the first parameter, in Alone condition
295 (recipient-absent), food was delivered in front of the recipient's cage as in Faced
296 condition (recipient-present), but it was removed by the experimenter after 10 s. For the
297 second parameter, the recipient was either the dominant (Heiji) or the subordinate
298 monkey (Theta). For the third parameter, in Unequal labor 1 and 2 conditions, the
299 operator obtained food by completing the sequence of pulling the handle of the support
300 board followed by opening the drawer; thus the operator had to complete 2 actions in
301 order to obtain food, whereas the recipient received food without any labor. In Equal
302 labor condition, first, the recipient pulled the handle of the support board in order to
303 enable the operator to pull the drawer of a container and then the operator pulled one of
304 the two containers. In other words, both operator and recipient contributed one action to
305 obtain food for each. In Alone condition of Equal labor condition, however, the
306 experimenter pulled the handle of the board in place of the recipient.
307 Subjects were tested in the following sequence: first, Unequal labor 1, second,
308 Equal labor, and third, Unequal labor 2 conditions in the ABA design. The reason why
309 we set two Unequal labor conditions and conducted each Unequal condition before and
310 after Equal condition was that we investigated whether the experience of others' labor
311 leading to food in Equal labor condition would influence the operators' subsequent food
312 choices. In all three conditions, the reward in the recipient side was either high- or

low-value food (see Figure 2). Left-right placement of food on the recipient's side was counterbalanced.

Experimental design

Each test session consisted of 10 trials. Each operator received 30 Faced (recipient-present) sessions and 30 Alone (recipient-absent) sessions. These two types of sessions were run alternatingly, one session per day. All operators started with the Alone condition. The recipients participated in two sessions every other day when Faced conditions were tested. The dominant and subordinate recipients were alternated every 10 sessions. The subjects' labor was changed after 20 and 40 sessions. All operators participated in this sequential order: Unequal labor 1, Equal labor and Unequal labor 2 condition.

Analysis

The experimenter recorded the operator's choices of container and any begging behaviors by the recipient on each trial. The records were confirmed from the videotapes later.

First, we examined the average frequency of operator choices for the high-value container in three separate two-way repeated ANOVAs with the presence of the recipient and social rank of the recipient (dominant/subordinate) as factors for the subjects' labor conditions. Additionally, we examined the average difference in frequency of operator choices for the high-value container between the Faced and Alone conditions in a two-way repeated ANOVA with the subjects' labor and the social rank of the recipient as factors.

Second, we measured recipient begging behaviors for the high-value food container, including after operator choices for the low-value food container, as a possible indicator of frustration. Each average ratio of those behaviors was examined in a two-way repeated ANOVA with the social rank of the recipient and labor as factors.

All analyses were conducted using SPSS version 17.0. The Bonferroni correction was applied for post-hoc comparisons.

Results

Figures 3a, 3b, 3c

Figure 3 shows the average number of operator choices for the high-value food container in Unequal labor 1 (Figure 3a), Equal labor (Figure 3b) and Unequal labor 2 conditions (Figure 3c). In Unequal 1 and 2 conditions, no main effect or interaction was significant. However, in Equal labor condition the main effect of presence of the recipient was significant [$F_{1,3}$=45.485, p=0.007]. No other main effect or interaction was significant. The difference in the average number of operator choices for the high-value food container between Faced and Alone conditions is presented in Figure S1 in Electronic Supplementary Material. This subtracted value is hereafter referred to as the operators' generosity score. The main effect of the labor was significant [$F_{2,6}$=14.211, p=0.005]. Post-hoc comparisons revealed a significant difference only between Equal and Unequal labor 2 conditions [p=0.035]. No other main effects or interactions were significant.

Figure 4

Figure 4 shows the average ratio of recipient begging behaviors for the high-value food container. The main effect of the labor was significant [$F_{2,6}$=35.025, p=0.000]. Post-hoc comparisons revealed significant differences between Unequal labor 1 and Equal labor conditions [p=0.030], and Equal and Unequal labor 2 conditions [p=0.028]. However, there was no difference between Unequal 1 and 2 conditions. No other main effect or interaction was significant.

Figure 5

Figure 5 shows the average ratio of recipient begging behaviors for the high-value food container after operators chose the low-value food container. This ratio is hereafter referred to as the recipients' frustration score. The main effect of the labor was significant [$F_{2,6}$=14.541, p=0.005]. Post-hoc comparisons revealed a significant difference only between Equal and Unequal labor 2 conditions [p=0.010]. Moreover, although the main effect of recipient's social rank was not significant, there was a significant interaction between social rank of recipient and labor [$F_{2,6}$=7.110, p=0.026]. This interaction means that, only in Unequal labor 1 condition, the dominant recipient more frequently begged for the high-value food container after operators chose the low-value food container than the subordinate recipient, though there was no difference between the ratios of both recipients' begging behaviors in the other labor conditions.

Both the operators and the recipients ate the high-value food whenever it was given, whereas the recipients almost always refused to receive the low-value food

regardless of the subjects' labor conditions. The average ratio of recipient receiving the low-value food is presented in Figure S2 (a: Dominant recipient condition / b: Subordinate recipient condition) in Electronic Supplementary Material.

Discussion

In the present study, operator monkeys chose the high-value food container significantly more often when a conspecific recipient was present (Faced condition) than absent (Alone condition) only when the recipients helped them to operate the containers (Equal labor condition), irrespective of the social rank of the recipient. On the other hand, when operators alone had to work for food while recipients received food without any labor (Unequal labor 1 and 2 conditions), operators did not change their food sharing strategies as a function of the presence or social rank of the recipient. Additionally, they chose the high-value container for both recipients significantly more often in Equal labor condition than in Unequal labor 2 condition. These results clearly show that capuchin monkeys are sensitive to others' labor and may change how they distribute rewards depending upon others' contribution to the task. Moreover, operators were more likely to give their partner the low-value food in Unequal labor 2 compared to Unequal labor 1 condition, though not significantly so. Thus, the data imply a weak contrast effect based on whether the partner had to help previously. In other words, the operators may have been frustrated by witnessing recipients receiving food without any labor, after experiencing the same helpful partner.

In de Waal & Berger (2000), food sharing could have been a byproduct of increased proximity between the monkeys, rather than an intention of the operator. This account fails to apply to our study, since the operator monkeys had to make a

409 dichotomous choice, and there was no increased proximity between operator and
410 recipient. The operators in the present study made choices that were at chance level
411 when the partner did not need to help, but actively tried to benefit their partner when
412 he/she did help.

413 Brosnan et al. (2010b) reported that the chimpanzees responded similarly when
414 the partner obtained the same reward as they did for 'free' versus when both individuals
415 had to exchange to receive the reward. This finding is in accord with Fontenot et al.
416 (2007) and van Wolkenten et al. (2007), which showed capuchins' failure to respond to
417 differences in effort only. Such studies in which each individual's task was independent
418 indicate that difference in effort alone is insufficient to evoke a response to inequity. On
419 the other hand, Brosnan et al. (2006) investigated how capuchins would react to
420 inequitable rewards by a joint task, as our study, which required the individuals to pull a
421 bar together in order to receive food. They reported that capuchins' cooperation success
422 depended not on the equity of the reward distribution, but on the equity of the partner's
423 behavior. In other words, equitable capuchin dyads in which the individuals regularly
424 alternated taking the higher-value reward in an unequal distribution were more than
425 twice as successful as less-equitable dyads. Studies in which each individual's task was
426 dependent, as Brosnan et al. (2006) and our study, suggest that perceived effort is more
427 crucial in joint tasks for capuchin monkeys. This suggestion seems consistent with the
428 idea that reciprocity appears crucial for participants to maintain cooperation in food
429 sharing situations. Indeed, capuchin monkeys, like chimpanzees, are capable of
430 contingent reciprocity in an alternating condition (Hattori et al. 2005), though it may be
431 difficult for them to succeed by spontaneous alternation of donor and recipient roles
432 (capuchin monkeys: Pelé et al. 2010; chimpanzees: Yamamoto & Tanaka 2009). Future

studies should ask whether reciprocity facilitates capuchins' prosocial food sharing by exchanging their role in order to test the effect of reciprocity for their prosociality.

One possible explanation for our results in Equal condition is that the recipients waited to manipulate the apparatus until the operator was standing in front of the high-value container. This could have led to the outcome we see, in which high-value rewards are pulled more in the equal labor condition. However, we do not think this explanation applies in our case, as recipients in fact almost always pulled the handle of the support board as soon as the screen was removed. That is, recipients did not work with precise timing. Conceivably, the recipients' begging behaviors might be a form of harassment claiming the operators to share high-value food. Stevens (2004) reported that begging behaviors (harassment) can play a significant role in food sharing in chimpanzees and squirrel monkeys. In our previous study (Takimoto et al. 2010), blocking visual contact between the operator and the recipient resulted in the operators generally shifting toward giving the low-value food to the recipients, so the latter's begging behaviors may have sustained more prosocial food sharing by operators. If this applied to the present study, recipients should have shown more begging behaviors in Equal labor condition than in Unequal labor 1 and 2 conditions; however, the opposite trend was observed in fact. This result suggests that operator choices of the high-value food for recipients were not just a reaction to recipients' begging signals.

In our previous study (Takimoto et al. 2010), the same operator monkeys chose the high-value food container for the subordinate recipient more frequently than when the recipient was absent, even though the recipient received food without any labor. In the present study, however, they did not choose the high-value container for recipients more than when they were alone in Unequal labor conditions. This may be because of a

457 difference in the operators' own labor to obtain food. Previously (Takimoto et al. 2010),
458 operators had only to pull the handle of the drawer of the container to obtain food, that
459 is, only one action was required of them. On the other hand, in Unequal labor conditions
460 of the present study, double actions were required of operators: pulling the handle of the
461 board and pulling the drawer of the selected container. Therefore, in Unequal labor
462 conditions, rather, it was expected the operators should have show inequity aversion by
463 choosing the high-value container significantly less frequently in the presence of the
464 recipient than in his/her absence if capuchin monkeys are sensitive to others' labor.
465 Contrary to this hypothesis, the operators failed to show such a tendency in Unequal
466 labor conditions, though they were slightly below chance in giving high-value food in
467 Unequal labor 2 condition.

468 However, this result does not necessarily mean lack of inequity aversion in
469 capuchin monkeys. Capuchins are not only suggested to have inequity aversion in
470 previous studies (Brosnan & de Waal 2003; Brosnan et al. 2010a; Fletcher 2008;
471 Takimoto et al. 2010; van Wolkenten et al. 2007) but also shown robust other-regarding
472 preferences in experimental tasks involving food-sharing (Lakshminarayanan & Santos
473 2008, Takimoto et al. 2010), token exchange (de Waal et al. 2008) and bar-pulling
474 (Brosnan et al. 2010a). Therefore, it appears difficult for them to maintain perfect equity
475 in every interaction because it is also hard to produce prosocial behavior without some
476 degree of inequity tolerance (Brosnan et al. 2010a). In fact, the evolution of human
477 society and economic growth are often accompanied by inequality (Aghion et al. 1999),
478 leaving open the possibility that prosocial motivations must entail inequity tolerance if
479 they are to result in extensive cooperation.

480 Recipients continued to cooperate by repositioning the food containers, even

481 though this might not necessarily lead to the high-value food for them in the equal labor
482 condition. This may have been because the operators chose the high-value food
483 container for both recipients in 65-70% of trials, probably enough to maintain the
484 recipients' motivation to continue cooperating, given the species' natural social
485 tolerance. Capuchin monkeys are reported to donate food to conspecifics (de Waal
486 1996); such active giving of food has also been observed in our group, involving
487 unrelated individuals (Hattori, unpublished video recording). Capuchin monkeys are not
488 cooperative breeders, unlike common marmosets and cottontop tamarins, although they
489 show allonursing (Baldovino and Di Bitetti 2008, Fragaszy et al. 2004). Moreover, our
490 capuchins also have lived together for over 8 years. Cronin et al. (2009) reported that
491 cottontop tamarins (*Saguinus oedipus*) who were housed together for at least 5 years
492 continued to cooperate under unequal rewards, but they were sensitive to reward
493 distributions and cooperated most often when both individuals receive rewards either
494 simultaneously or over repeated interactions. Brosnan et al. (2005) showed that
495 chimpanzees with long-term relationships were more tolerant of inequitable reward
496 distributions.

497 We also found that recipients showed more begging behaviors for the
498 high-value food container after operator choices for the low-value container especially
499 in Equal labor condition compared to Unequal labor 2 condition, but not Unequal labor
500 1 condition. In other words, the recipient's experience of helping the operator on the
501 task in Equal labor condition reduced their begging behaviors after operator choices for
502 the low-value container in the unequal labor 2 condition, even though Unequal 1 and 2
503 conditions were identical. This result suggests that not only operators but also recipients
504 are sensitive to their own as well as others' reward and labor and can adjust their

behaviors flexibly in a cooperative food sharing situation, that is, recipients may not expect to receive the high-value food without any labor, and experience frustration by not receiving the high-value food after their experience of being rewarded in return for helping others. Indeed, Lakshminarayanan and Santos (2009) reported that capuchins easily inhibit the tendency to reach directly for food in an object retrieval task, successfully employing an alternative reaching strategy that allows them to achieve good retrieval performance. Additionally, we have demonstrated that capuchins are capable of delaying of gratification by waiting until additional food items had accumulated before reaching for the food, thereby increasing the total amount obtained (Anderson et al. 2010), changing their requesting actions flexibly in response to changes in the experimenter's attention (Hattori et al. 2010) and modifying their own behaviors according to a conspecific's emotional expressions (Morimoto and Fujita in press). All of these relevant studies convergingly support capuchins' sensitivity to others' behavior and behavioral flexibility.

In conclusion, this is the first study to have shown that capuchin monkeys, not only operators but also recipients, are sensitive to others' labor and behave flexibly based on their own experience in a cooperative food sharing situation. More specifically, operator monkeys actively distributed better food to the recipient if he/she helped them to access rewards in the joint task. Our study indicates that perceived effort may be more crucial in joint tasks for capuchin monkeys and shows that joint tasks are particularly useful to explore the origin of inequity aversion in nonhuman primates. However, it is still unknown whether capuchins are aware of the amount of others' effort and whether they compare the cost/benefit relationship between self and others. Future work may vary the amount of recipient labor with the operator labor kept

constant.

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553 **References**

554 Aghion E, Caroli E, Garcia-Penalosaand C (1999) Inequality and economic growth: The
555 perspective of the New Growth Theories. J Econ Lit 27:1615-1660

556 Anderson JR (2007) Animal behavior: tolerant primates cooperate best. Curr Biol 17(7):
557 R242-R244

558 Anderson JR, Hattori Y, Fujita K (2008) Quality before quantity: rapid learning of
559 reverse-reward contingency by capuchin monkeys (*Cebus apella*). J Comp Psychol
560 122(4):445-448

561 Anderson JR, Kuroshima H, Fujita K (2010) Delay of gratification in capuchin
562 monkeys (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). J Comp Psychol
563 124(2):205-210

564 Anderson JR, Kuroshima H, Hattori Y, Fujita K. (2005a) Attention to combined
565 attention in New World monkeys (*Cebus apella, Saimiri sciureus*) J Comp Psychol
566 119(4):461–464

567 Anderson JR, Kuroshima H, Kuwahata H, Fujita K (2004) Do squirrel monkeys
568 (*Saimiri sciureus*) and capuchin monkeys (*Cebus apella*) predict that looking leads
569 to touching? Anim Cogn 7(3):185-192

570 Anderson JR, Kuroshima H, Paukner A, Fujita K (2009) Capuchin monkeys (*Cebus*
571 *apella*) respond to video images of themselves. Anim Cogn 12(1):55-62

572 Anderson JR, Kuwahata H, Kuroshima H, Leighty K, Fujita K. (2005b) Are monkeys
573 aesthetists? Rensch (1957) revisited. J of Exp Psychol Anim Behav Process 31(1):
574 71–78

575 Baldovino MC, Di Bitetti MS (2008) Allonursing in tufted capuchin monkeys (*Cebus*
576 *nigritus*): milk or pacifier? Folia Primatol 79:79-92

577 Boyd RT, Richerson (2005) The origin and evolution of cultures. New York: Oxford
578 Bräuer J, Call J, Tomasello M (2006) Are apes really inequity averse? Proc R Soc Lond
579 B Biol Sci 273:3123-3128
580 Bräuer J, Call J, Tomasello M (2009) Are apes inequity averse? New data on the
581 token-exchange paradigm. Am J Primatol 71:175-181
582 Brosnan SF (2006) Nonhuman species' reaction to inequity and their implications for
583 fairness. Soc Justice Res 19:153-185
584 Brosnan SF, de Waal FBM (2003) Monkeys reject unequal pay. Nature 425:297-299
585 Brosnan S F, de Waal FBM (2006) Partial support for a non-replication: Commentary on
586 Roma, Silberberg, Ruggiero, and Suomi (2006). Journal of Comparative
587 Psychology 120(1): 74-75
588 Brosnan SF, Freeman C, de Waal FBM (2006) Partner's behavior, not reward
589 distribution, determines success in an unequal cooperative task in capuchin monkeys.
590 Am J Primatol 68:713-724
591 Brosnan SF, Houser D, Leimgruber K, Xiao E, Chen T, de Waal FBM (2010 a)
592 Competing demands of prosociality and equity in monkeys. Evol Hum Behav 31:
593 279-288
594 Brosnan SF, Schiff HC, de Waal FBM (2005) Tolerance for inequity may increase with
595 social closeness in chimpanzees. Proc R Soc Lond B Biol Sci 272:253-258
596 Brosnan SF, Talbot C, Ahlgren M, Lambeth SP, Schapiro SJ (2010b) Mechanisms
597 underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. Anim
598 Behav 79(6):1229-1237
599 Burkart JM, Fehr E, Efferson C, van Schaik CP (2007) Other-regarding preferences in a
600 non-human primate: Common marmosets provision food altruistically. Proc Natl

601 Acad Sci USA 104:19762-19766
602 Clutton-Brock T (2002) Breeding together: kin selection and mutualism in cooperative
603 vertebrates. Science 296:69-72
604 Crawford MP (1937) The cooperative solving of problems by young chimpanzees.
605 Comp Psychol Monogr 14:1-88
606 Cronin KA, Kurian AV, Snowdon CT (2005) Cooperative problem solving in a
607 cooperatively breeding primate (*Saguinus oedipus*). Anim Behav 69(1):133-142
608 Cronin KA, Schroeder KKE, Rothwell ES, Silk J (2009) Cooperatively breeding
609 cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term
610 mates. J Comp Psychol 123(3):231-241
611 Cronin KA, Snowdon CT (2008) The effects of unequal reward distributions on
612 cooperative problem solving by cottontop tamarins, *Saguinus Oedipus*. Anim Behav
613 75(1): 245-257
614 de Waal FBM (1996) Good natured: The origins of Right and Wrong in Humans and
615 Other Animals. Harvard Univ Press, Cambridge MA
616 de Waal FBM, Berger ML (2000) Payment for labour in monkeys. Nature 404:563-563
617 de Waal FBM, Leimgruber K, Greenberg AR (2008) Giving is self-rewarding for
618 monkeys. Proc Natl Acad Sci USA 105:13685-13689
619 de Waal FBM, Suchak M (2010) Prosocial primates: selfish and unselfish motivations.
620 Phil Trans R Soc B 365: 2711-2722
621 Dindo M, de Waal FBM (2007) Partner effects on food consumption in brown capuchin
622 monkeys. Am J Primatol 69:1-9
623 Dubreuil D, Gentile MS, Visalberghi E (2006) Are capuchin monkeys (*Cebus apella*)
624 inequity averse? Proc R Soc Lond B Biol Sci 273:1223-1228

625 Dugatkin (1997) Cooperation among animals. An evolutionary perspective. Oxford
626 University Press, Oxford
627 Fletcher GE (2008) Attending to the outcome of others: disadvantageous inequity
628 aversion in male capuchin monkeys (*Cebus apella*). Am J Primatol 70:901-905
629 Fontenot MB, Watson SL, Roberts KA, Miller RW (2007) Effects of food preferences
630 on token exchange and behavioural responses to inequality in tufted capuchin
631 monkeys, *Cebus apella*. Anim Behav 74(3):487–496
632 Fragaszy DM, Visalberghi E, Fedigan LM (2004) The complete capuchin: the biology
633 of the genus *Cebus*. Cambridge Univ Press, New York
634 Fujita K (2004). How do nonhuman animals perceptually integrate figural fragments?
635 Jpn Psychol Res 46:154-169
636 Fujita K, Giersch A (2005) What perceptual rules do capuchin monkeys (*Cebus apella*)
637 follow in completing partly occluded figures? J Exp Psychol Anim Behav Process
638 31(4):387-398
639 Fujita K., Kuroshima H, Asai S (2003) How do tufted capuchin monkeys (*Cebus*
640 *apella*) understand causality involved in tool use? J of Exp Psychol Anim Behav
641 Process 29(3): 233-242
642 Fujita K, Kuroshima H, Masuda T (2002) Do tufted capuchin monkeys (*Cebus apella*)
643 spontaneously deceive opponents? A preliminary analysis of an experimental
644 food-competition contest between monkeys. Anim Cogn 5(1):19-25
645 Fujita, K., Sato, Y., & Kuroshima, H. Learning and generalization of tool use by tufted
646 capuchin monkeys (*Cebus apella*) in tasks involving three factors: reward, tool, and
647 hindrance. (in press) J of Exp Psychol Anim Behav Process
648 Hare and Kwetuenda (2010) Bonobos voluntarily share their own food with others. Curr

649 Biol 20(5): R230-R231

650 Hattori Y, Kuroshima H, Fujita K (2005) Cooperative problem solving by tufted
651 capuchin monkeys (*Cebus apella*): spontaneous division of labor, communication,
652 and reciprocal altruism. J Comp Psychol 119(3):335-342

653 Hattori Y, Kuroshima H, Fujita K (2007) I know you are not looking at me: capuchin
654 monkeys' (*Cebus apella*) sensitivity to human attentional states. Anim Cogn 10(2):
655 141-148

656 Hattori Y, Kuroshima H, Fujita K (2010) Tufted capuchin monkeys (*Cebus apella*)
657 show understanding of human attentional states when requesting food held by a
658 human. Anim Cogn 13(1):87–92

659 Henrich J (2004) Inequity aversion in capuchins? Nature 428:139

660 Hirata S, Fuwa K (2007) Chimpanzees (*Pan troglodytes*) learn to act with other
661 individuals in a cooperative task. Primates 48:13-21

662 Jensen K, Hare B, Call J, Tomasello M (2006) What's in it for me? Self-regard
663 precludes altruism and spite in chimpanzees. Proc R Soc Lond B Biol Sci
664 273:1013-1021

665 Kuroshima H, Fujita K, Adachi I, Iwata K, Fuyuki A (2003) A Capuchin monkey
666 (*Cebus apella*) recognizes when people do and do not know the location of food.
667 Anim Cogn 6(4):283-291

668 Kuroshima H, Fujita K, Fuyuki A, Masuda T (2002) Understanding of the relationship
669 between seeing and knowing by tufted capuchin monkeys (*Cebus apella*). Anim
670 Cogn 5(1):41-48

671 Kuroshima H, Kuwahata H, Fujita K (2008) Learning from others' mistakes in capuchin
672 monkeys (*Cebus apella*). Anim Cogn 11(4):599-609

673 Lakshminarayanan VR, Santos LR (2008) Capuchin monkeys are sensitive to others'
674 welfare. Curr Biol 18(21):R999-R1000
675 Lakshminarayanan VR, Santos LR (2009) Cognitive preconditions for responses to
676 fairness: An object retrieval task in capuchin monkeys (*Cebus apella*). J Neurosci
677 Psychol Econ 2(1): 12-20
678 Melis AP, Hare B, Tomasello M (2006a) Engineering cooperation in chimpanzees:
679 tolerance constraints on cooperation. Anim Behav 72(2):275-286
680 Melis AP, Hare B, Tomasello (2006b) Chimpanzees recruit the best collaborators.
681 Science 311: 1297-1300
682 Melis AP, Warneken F, Jensen K, Schneider AC, Call J, Tomasello
683 M (in press) Chimpanzees help conspecifics obtain food and non-food items.
684 Proc R Soc Lond B Biol Sci
685 Morimoto Y, Fujita K (in press) Capuchin monkeys (*Cebus apella*) modify their own
686 behaviors according to a conspecific's emotional expressions. Primates
687 Neiworth JJ, Johnson ET, Whillock K, Greenberg J, Brown V (2009) Is a sense of
688 inequity an ancestral primate trait? Testing social inequity in cotton top tamarins
689 (*Saguinus oedipus*). J Comp Psychol 123(1): 10-17
690 Paukner A, Anderson JR, Fujita K (2004) Reactions of capuchin monkeys (*Cebus*
691 *apella*) to multiple mirrors. Behav Processes 66:1-6
692 Pelé M, Thierry B, Call J, Dufour V (2010) Monkeys fail to reciprocate in an
693 exchange task. Anim Cogn 13(5):745-51
694 Roma PG, Silberberg A, Ruggiero AM, Suomi SJ (2006) Capuchin monkeys, inequity
695 aversion, and the frustration effect. J Comp Psychol 120(1):67-73
696 Silberberg A, Crescimbene L, Addessi E, Anderson JR and Visalberghi E (2009) Does

697 inequity aversion depend on a frustration effect? A test with capuchin monkeys
698 (*Cebus apella*). Anim Cogn 12(3):505-509
699 Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP,
700 Mascaro J, Schapiro SJ (2005) Chimpanzees are indifferent to the welfare of
701 unrelated group members. Nature 437:1357-1359
702 Stevens JR (2004) The selfish nature of generosity: Harassment and food sharing in
703 primates. Proc R Soc B 21:451–456
704 Stevens JR (2010) Donor payoffs and other-regarding preferences in cotton-top
705 tamarins (*Saguinus oedipus*). Anim Cogn 13(4):663-70
706 Takimoto A, Kuroshima H, Fujita K (2010) Capuchin monkeys (*Cebus apella*) are
707 sensitive to others' reward: an experimental analysis of food-choice for conspecifics.
708 Anim Cogn 13(2):249-261
709 van Wolkenten M, Brosnan SF, de Waal FBM (2007) Inequity responses of monkeys
710 modified by effort. Proc Natl Acad Sci USA 104:18854-18859
711 Vonk J, Brosnan SF, Silk JB, Henrich J, Richardson AS, Lambeth SP, Schapiro SJ,
712 Povinelli DJ (2008) Chimpanzees do not take advantage of very low cost
713 opportunities to deliver food to unrelated group members. Anim Behav 75(5):
714 1757-1770
715 Wynne CDL (2004) Fair refusal by capuchin monkeys. Nature 428:140
716 Yamamoto S, Tanaka M (2009) Do chimpanzees (*Pan troglodytes*) spontaneously take
717 turns in a reciprocal cooperation task? J Comp Psychol 123(3):242-249
718 Yamamoto S, Tanaka M (2010) The influence of kin relationship and reciprocal context
719 on chimpanzees' other-regarding preferences. Anim Behav 79(3):595-602
720

721 **Table**

722

723 **Table 1** The test sequence in each experiment. Each cell shows the social rank of the
724 recipient. This procedure was conducted in a counterbalanced order across the
725 operators.

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session	1~10	11~20	21~30	31~40	41~50	51~60
labor	Unequal 1		Equal		Unequal 2	
operator	recipient					
Pigmon	Subordinate	Dominant	Subordinate	Dominant	Subordinate	Dominant
Zilla	Dominant	Subordinate	Dominant	Subordinate	Dominant	Subordinate
Zinnia	Dominant	Subordinate	Dominant	Subordinate	Dominant	Subordinate
Kiki	Subordinate	Dominant	Subordinate	Dominant	Subordinate	Dominant

Table 1

Figures

Figure 1 The experimental setup in Unequal labor condition (a) and Equal labor condition (b). In Unequal labor condition (a), the operator had to first pull the handle of the support board and then pull the drawer of one container. The recipient received food passively. In Equal labor condition (b), the recipient had to pull the handle of the board in order to enable the operator to operate the drawer of a container. Then, the operator pulled the drawer of one container.

Figure 2 The placement of food for the operator and the recipient in each condition in all experiments. “H” denotes the high-value food and “L” denotes the low-value food.

Figure 3 The average number of operator choices for the high-value food container in Unequal labor 1 condition (a), in Equal labor condition (b) and in Unequal labor 2 condition (c). The x axis shows the experimental condition and the y axis shows the average number of choices. The left pair of bars in each figure is for Dominant recipient condition and the right pair of bars is for Subordinate recipient condition. Symbols denote individuals. Each bar and each symbol is based on 10 trials (= the number of trials per session).

Figure 4 The average ratio of recipient begging behaviors for the high-value food container in Dominant and Subordinate recipient conditions. The x axis shows the experimental condition and the y axis shows the average ratio of recipient begging behaviors. The left half of bars is for Dominant recipient condition and the right half of bars is for Subordinate recipient condition. Symbols denote individuals whom recipients

788 begged for the high-value food (operators). Each bar and each symbol is based on 10
789 trials (= the number of trials per session).
790
791 **Figure 5** The average ratio of recipient begging behaviors for the high-value container
792 after operator choices for the low-value food container in Dominant and Subordinate
793 recipient conditions. The x axis shows the experimental condition and the y axis shows
794 the average ratio of recipient begging behaviors. The left half of bars is for Dominant
795 recipient condition and the right half of bars is for Subordinate recipient condition.
796 Symbols denote individuals whom recipients begged for the high-value food (operators).
797 Each bar and each symbol is based on 10 trials (= the number of trials per session).
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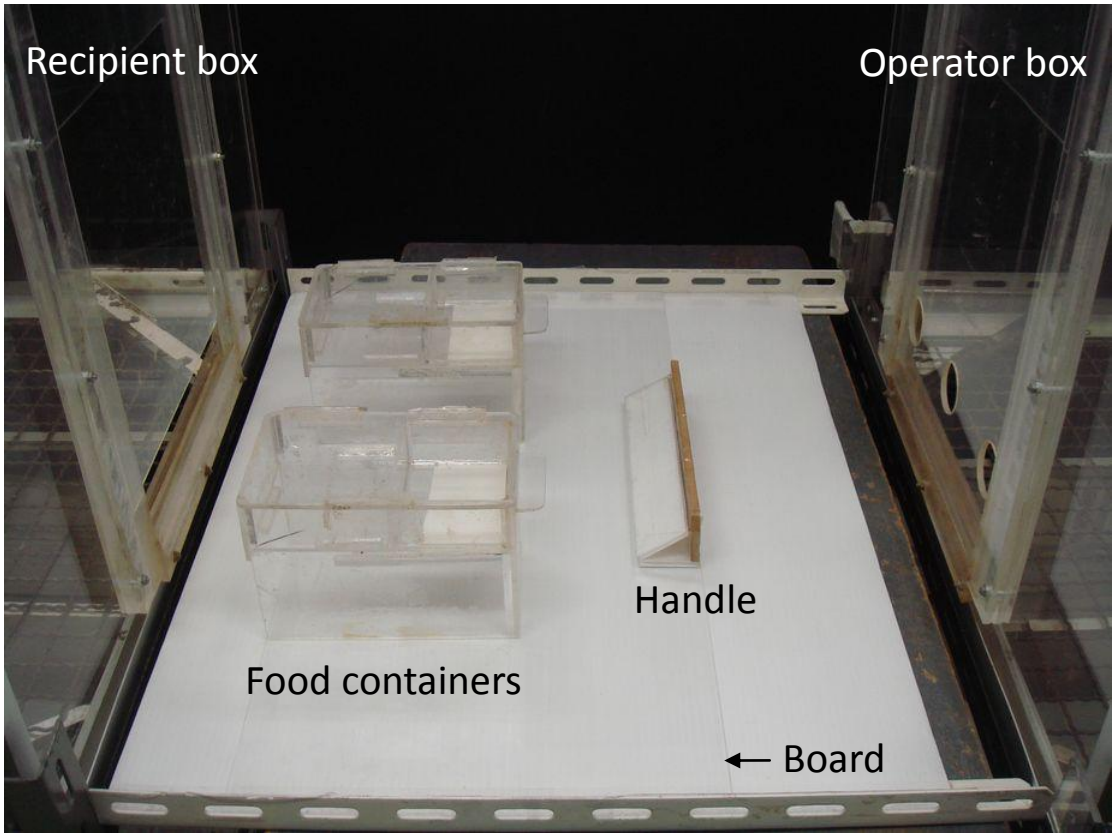


Figure 1a

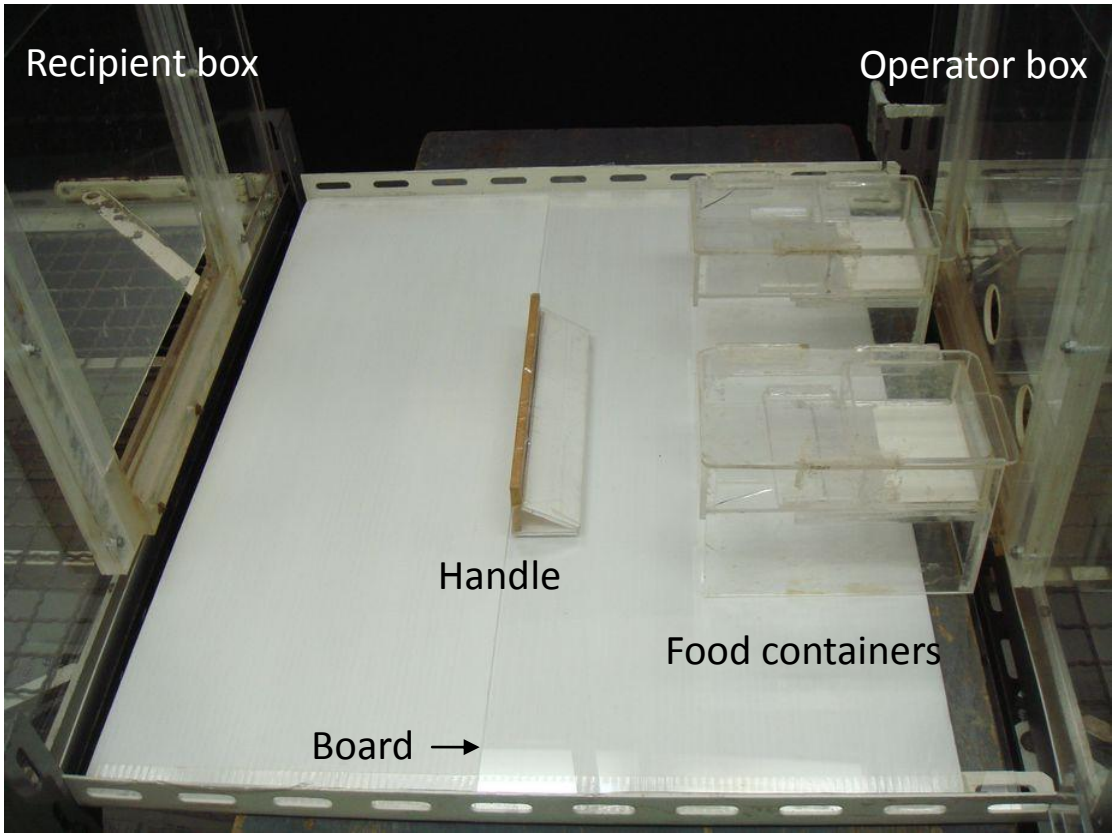
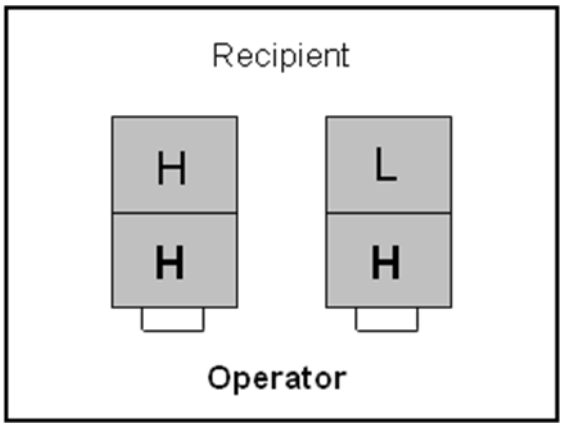


Figure 1b



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828 **Figure 2**

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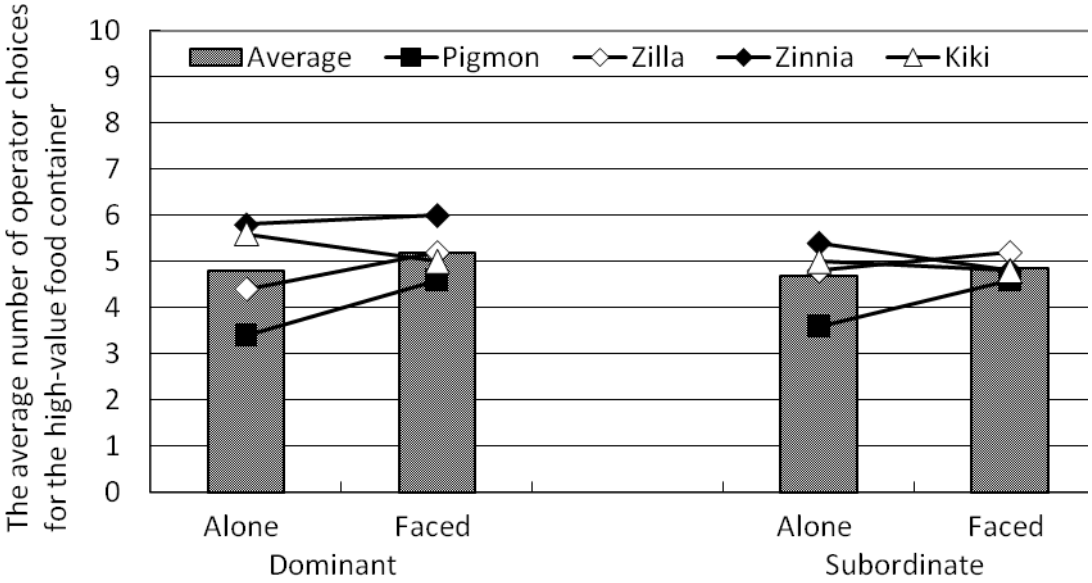

Figure 3a

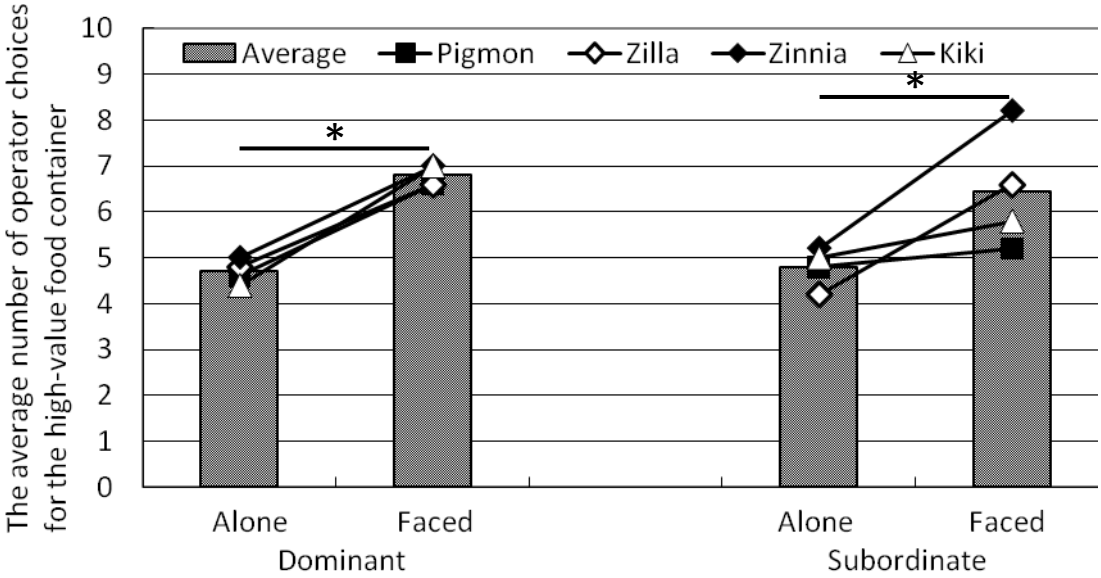

Figure 3b

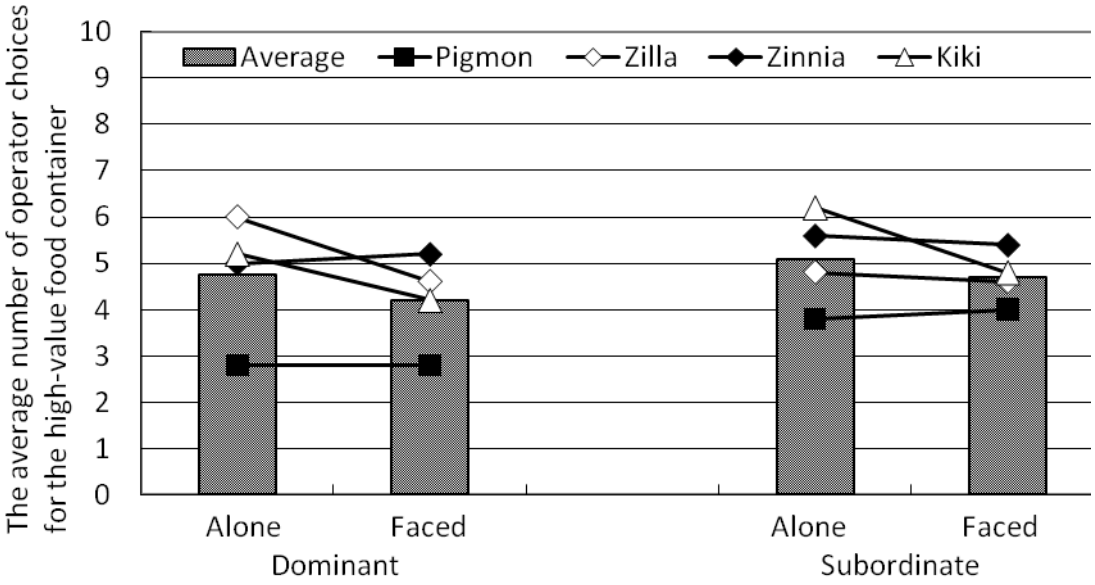

Figure 3c

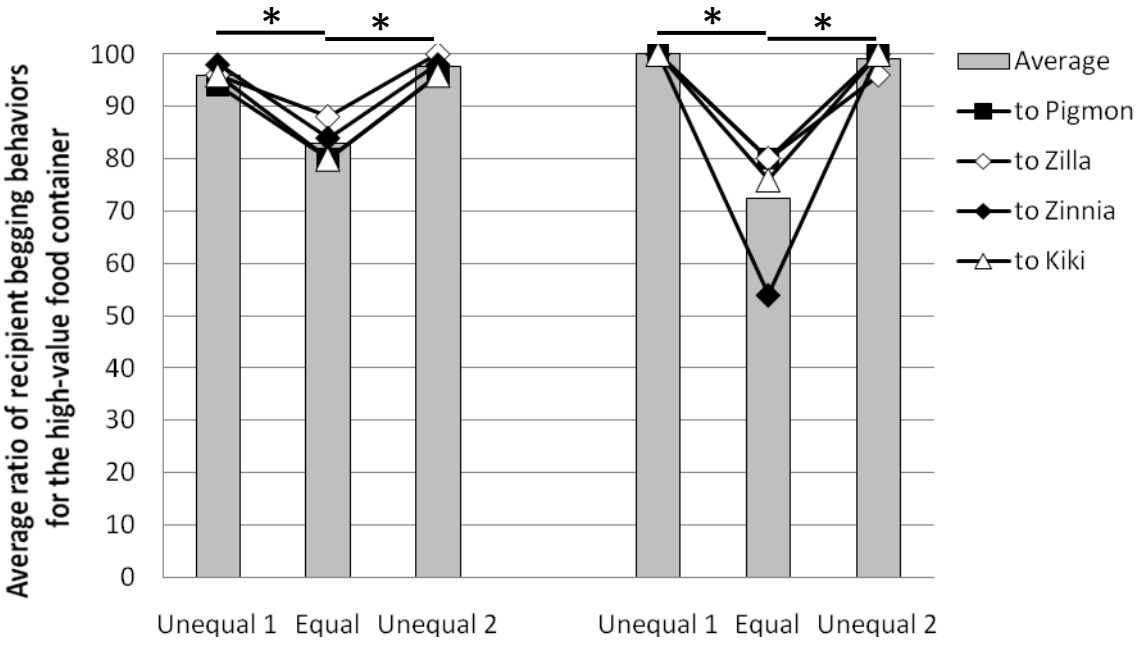

Figure 4

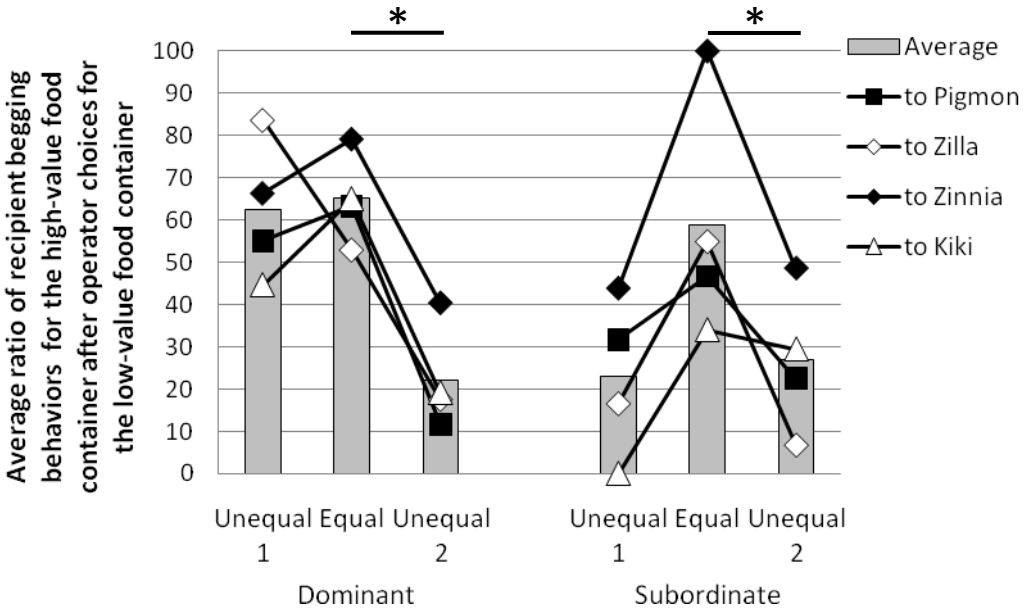

Figure 5